Biological Conservation 143 (2010) 2229–2237

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Assessing critical habitat: Evaluating the relative contribution of habitats to population persistence

Julie A. Heinrichs [a,*], Darren J. Bender [a,1], David L. Gummer [b], Nathan H. Schumaker [c]

[a] University of Calgary, 2500 University Drive NW Calgary, Alberta, Canada T2N 1N4
[b] Parks Canada, Western and Northern Service Centre, 1550-635, 8 Avenue SW Calgary, Alberta, Canada T2P 3M3
[c] Western Ecology Division, US EPA, 200 SW 35th St. Corvallis, OR 97333, USA

ARTICLE INFO

Article history:
Received 18 February 2010
Received in revised form 2 June 2010
Accepted 8 June 2010
Available online 3 July 2010

Keywords:
Alberta, Canada
Dipodomys ordii
Habitat quality
Occurrence
Persistence
Population viability
Source–sink dynamics
Spatially-explicit population model
Species at risk

ABSTRACT

A principal challenge of species conservation is to identify the specific habitats that are essential for long-term persistence or recovery of imperiled species. However, many commonly used approaches to identify important habitats do not provide direct insight into the contribution of those habitats to population persistence. To assess how habitats contribute to overall population viability and characterize their relative importance, a spatially-explicit population viability model was used to integrate a species occurrence model with habitat quality and demographic information to simulate the population dynamics of the Ord's kangaroo rat (*Dipodomys ordii*) in Alberta, Canada. Long-term productivity (births–deaths) in each patch was simulated and iterative patch removal experiments were conducted to generate estimates of the relative contribution of habitat types to overall population viability. Our results indicated that natural dune habitats are crucial for population viability, while disturbed/human-created habitats make a minor contribution to population persistence. The results also suggest that the habitats currently available to Ord's kangaroo rats in Alberta are unlikely to support long-term persistence. Our approach was useful for identifying habitats that did not contribute to population viability. A large proportion of habitat (39%) represented sinks and their removal increased estimated population viability. The integration of population dynamics with habitat quality and occurrence data can be invaluable when assessing critical habitat, particularly in regions with variable habitat quality. Approaches that do not incorporate population dynamics may undermine conservation efforts by under- or over-estimating the value of habitats, erroneously protecting sink habitats, or failing to prioritize key source habitats.

1. Introduction

A principal challenge of species conservation is to identify the specific habitats that are essential for long-term persistence or recovery of endangered species. Habitat destruction as a result of loss, degradation, and fragmentation often increases the heterogeneity and complexity of landscapes, and complicates decisions as to which habitats should be protected or restored. Several approaches for identifying important habitats have been used, yet they often do not provide clear insight into the population viability consequences of protecting one habitat versus another.

Many studies have assessed habitat use by evaluating occurrence data or associating the presence/abundance of a species with local resources (e.g. Boyce et al., 2003; Carroll et al., 2001; Johnson et al., 2004). However, there are several limitations of using species occurrence data and associated models for identifying essential habitats. Such approaches often assume that short-term data represent the typical state of the population, which may be inappropriate particularly if populations cycle or fluctuate stochastically through time (Armstrong, 2005; Garshelis, 2000). Patterns of occurrence, particularly abundance, may also be misleading indicators of local habitat productivity (Garshelis, 2000) and habitat quality (Battin, 2004; Van Horne, 1983). Aldridge and Boyce (2007) caution of a potential situation where habitat models identify high levels of species occurrence within sink habitats, wherein mortality exceeds survival and/or reproductive rates (Pulliam, 1988). In such cases, high species occurrence is sometimes interpreted to mean 'important' habitat for the species, yet these habitats may not contribute to population persistence or may even jeopardize long-term population viability.

The integration of population data, such as site-specific mortality or reproduction rates with occurrence models, provides a means of assessing relative habitat quality and refining habitat

* Corresponding author.
E-mail addresses: j.a.heinrichs@gmail.com (J.A. Heinrichs), dbender@ucalgary.ca (D.J. Bender).
[1] Address: Department of Geography, University of Calgary, 2500 University Drive NW Calgary, Alberta, Canada T2N 1N4. Tel.: +1 403 220 6398.

0006-3207/$ - see front matter © 2010 Elsevier Ltd. All rights reserved.
doi:10.1016/j.biocon.2010.06.009

conservation priorities (e.g. Aldridge and Boyce, 2007; Falcucci et al., 2009; Nielsen et al., 2006). Yet such approaches cannot directly link local habitat attributes or population performance with regional population viability and therefore do not necessarily identify habitats that have key roles in population persistence.

Local population dynamics, productivity, and persistence may be influenced by patch quality and quantity (e.g. patch size), as well as the spatial effects resulting from patch shape, orientation, and isolation (Bowman et al., 2002; Fleishman et al., 2002; Franken and Hik, 2004). Thus, in heterogeneous landscapes it is likely that individual habitat patches make unequal contributions to regional population persistence. Therefore, the process of assessing which habitats are biologically critical may require the integration of species occurrence mapping, habitat quality studies, population studies, and spatially-explicit population viability analysis.

We present a habitat- and demographic-based approach for identifying and prioritizing habitats that are essential for the persistence of populations. In this approach, habitat characteristics and population dynamics are integrated using population simulation, and the outcomes of the model are used to assess the contribution of individual or aggregate habitat patches to regional population persistence. This approach may be particularly useful when identifying important habitats for dynamic populations in heterogeneous landscapes, especially when habitat quality is variable. The long-term importance of currently unoccupied habitat patches can also be assessed using a population viability modeling approach, allowing a more comprehensive landscape assessment than would be possible using demographic rates alone. Where long-term field data are lacking, simulations also allow the investigation of the effects of environmental stochasticity or directional landscape change on cumulative patch occupancy and productivity. We demonstrate this approach using the Ord's kangaroo rat as a case study.

1.1. Case study

The Ord's kangaroo rat (*Dipodomys ordii*) is the only species of kangaroo rat to occur within Canada and its distribution is limited to one small region (a cluster of active sand dune complexes) in south-eastern Alberta and south-western Saskatchewan (COSEWIC, 2006). This is a disjunct population at the northernmost periphery of the species' range (Gummer, 1997; Kenny, 1989), isolated from the nearest conspecifics in Montana by a distance of approximately 270 km (COSEWIC, 2006). Small population size, geographic isolation, extreme fluctuations in population size, and rapid loss and degradation of natural habitat have led to the identification of this species as *endangered* in Canada (COSEWIC, 2006). The majority (76%) of kangaroo rat habitats in Alberta are

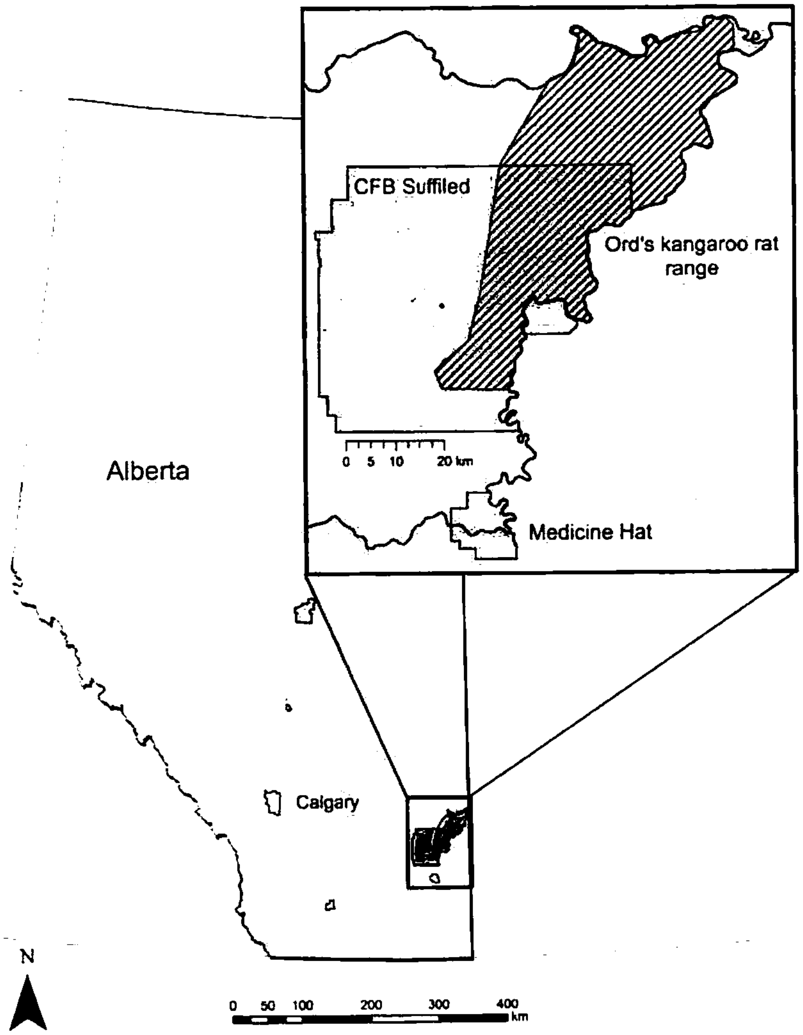

Fig. 1. Known range of Ord's kangaroo rats in Alberta, Canada (adapted from Alberta Ord's Kangaroo Rat Recovery Team, 2005).

located within Canadian Forces Base (CFB) Suffield, primarily (68%) in the Suffield National Wildlife Area (SNWA). The range of the Alberta population extends northward from CFB Suffield into surrounding agricultural lands which comprise 24% of kangaroo rat habitats in Alberta (Fig. 1; Alberta Ord's Kangaroo Rat Recovery Team, 2005; COSEWIC, 2006).

The Ord's kangaroo rat has specific habitat requirements for open, sparsely vegetated, sandy habitats to support its burrowing and hopping style of locomotion (Armstrong, 1979; Bartholomew and Caswell, 1951; Gummer, 1999; Hallett, 1982; Kenny, 1989). In Canada, natural habitats consist of discrete sandy features such as actively eroding sand dunes or blowouts. Kangaroo rats also occupy semi-stabilized or stabilized sand dunes where encroaching vegetation has limited the amount of open sand. However, in Canada the species has not been found in fully stabilized sand dune complexes (Kenny, 1989). To a lesser extent, kangaroo rats also inhabit exposed sandy soils not associated with sand dunes, often in areas where sand has been exposed by human activities (Gummer, 1997, 1999; Kaufman and Kaufman, 1982; Nero and Fyfe, 1956; Smith and Hampson, 1969; Stangl et al., 1992). Such anthropogenic habitats include sandy roads, trails, plowed fireguards, bare ground associated with oil and gas fixtures, and the margins of cultivated agricultural lands (COSEWIC, 2006). These areas are subject to human disturbances (e.g. traffic, grading), have higher rates of predation risk and parasitism than natural sites, and are often dominated by invasive plant species that may alter the diet composition of kangaroo rats (COSEWIC, 2006). Road-side habitats are also characterized by greater soil compaction, colder burrow temperatures, and lower overwinter survival rates than active sand dunes (Teucher, 2007).

Our case study is based on the Alberta population of the Ord's kangaroo rat for which we have approximately 15 years of recent population information. This population can be characterized as highly dynamic, experiencing substantial seasonal and inter-annual fluctuations (COSEWIC, 2006). Intra-annual population declines of an order of magnitude (i.e. $\leqslant 10\%$ survival) during winter have been observed (Gummer, 1997; Gummer and Robertson, 2003b; Kenny, 1989) and local extinctions in habitat patches (e.g., individual sand dunes or road segments) are common (Gummer and Robertson, 2003b; Kenny, 1989). Environmental fluctuations as well as high seasonal reproductive rates could lead to opportunistic increases in population density in marginal habitats, especially during the summer months when the environment becomes temporarily favorable (Van Horne, 1983). Thus, local occurrence or animal density may represent a poor indicator of the importance of occupied habitats to population persistence.

Recent research examining habitat selection by kangaroo rats in Alberta (Bender et al., 2010) produced an occurrence-based model of habitat use. The model was based on 2 years of standardized population monitoring data (see Bender et al., 2007), a resource selection function (RSF) approach (Boyce and McDonald, 1999; Manly et al., 2002), and its main output was a predicted occurrence map. While the model was robust, highly selective, and performed well in validation tests, the majority of habitats identified by the model are anthropogenic habitat features (roads) where kangaroo rats are known to exhibit high mortality and low productivity. In contrast, natural features (active sand dunes) that represent more productive habitats comprised a relatively small proportion of the habitat predicted to have high occurrence. The researchers remarked that it could not be used to directly assess critical habitat for the species as many locations with high probability of occurrence were low quality habitats, possibly serving as population sinks (Bender et al., 2010). Here we demonstrate how a predicted occurrence model can be integrated with information on habitat quality and population dynamics to identify specific habitat components (e.g., map pixels or habitat patches) that are expected to contribute to the long-term productivity and persistence of a population. For the purposes of assessing critical habitat from a biological perspective, such information should be more useful for evaluating and prioritizing habitat than simple maps that predict occurrence alone.

2. Methods

2.1. Overview

A spatially-explicit individual-based population model was used to link landscape structure from the habitat model with habitat quality and population dynamics. This approach provides a general method for identifying some of the biologically important elements of critical habitat such as individual or groups of breeding habitat patches that make a substantive contribution to long-term regional population persistence. Our use of the term critical habitat is consistent with its biological origins; however, this approach may also be useful for the identification of critical habitat within a legal context, for example under the Canadian Species At Risk Act or US Endangered Species Act. Our approach is based on knowledge of species-habitat relations (e.g., from a resource selection model) and demographic information (e.g., fecundity and habitat-specific survival). The process is entirely spatially-explicit such that information about landscape composition and configuration, including effects of patch size, inter-patch distance, and barriers to movement, can be incorporated in the assessment. The outcomes of the process are spatially-explicit vital rates, namely the long-term productivity of habitats, which indicate the contribution of each unit of habitat within the model. Thus, a direct comparison of habitat units (e.g. patches) can be made for diagnostic purposes or to rank and prioritize habitats. Scenarios of landscape change, such as habitat patch removals or additions, can be used to further investigate the importance of habitats (e.g., to generalize about the contribution of specific habitat types). As the modeling process incorporates elements of population viability analysis to provide estimates of extinction risk for each modeling scenario, this approach allows one to explore the implications of habitat modification and make inferences about the general roles of habitat types in affecting population persistence. We illustrate this approach and the useful information it generates in a case study of the Ord's kangaroo rat in Alberta, Canada.

2.2. Habitat model

An RSF-based habitat-occurrence model was developed for the Ord's kangaroo rat in Alberta as part of the recovery planning process (Bender et al., 2010). From this starting point, we sought to incorporate demographic information, such as fecundity and habitat-specific survival with the RSF-derived habitat map. A threshold probability of occurrence value representing 2/3 of the kangaroo rat occurrences (validated from an independent dataset collected in 2004–2005; Teucher, 2007) was used to classify the occurrence map into regions of either breeding habitat or non-habitat. Habitat was further classified into four types: active dune, semi-stabilized dune, road margins, or exposed sandy soils (generally the steep valley slopes of the South Saskatchewan River) using air photo interpretation and knowledge of features on the ground. The relative quality of active dune and road-side habitat types was estimated using habitat-specific overwinter survival rates (derived from Teucher, 2007), while the quality of the semi-stabilized sand dunes and exposed soil habitats was inferred from distribution data and expert knowledge (R. Dzenkiw, Lead Surveyor for Alberta Long-term Population Monitoring Program). Values for relative habitat quality of the different habitat types are provided in Table

Table 1
Broad habitat types and their relative habitat quality values.

Habitat type	Quality value
Active sand dune	100
Semi-stable sand dune	60
Road margins	56
Exposed, sandy river valley slopes	30

1. A range of semi-stabilized dune quality values was explored in a sensitivity analysis as a means of exploring the influence of parameter uncertainty on model outcomes. Habitat fragments of similar quality (e.g. natural versus road) that were within 30 m of each other were combined into one functional patch, resulting in 8413 habitat patches.

2.3. Population model

The spatially-explicit population model HexSim (PATCH version 1.3.6.9; Schumaker, 1998, 2008) was used to integrate the occurrence model with kangaroo rat population dynamics and estimate long-term habitat productivity and population viability. HexSim is an individual-based model which simulates population dynamics through time, recording individual births, deaths, and reproduction, as well as explicit movement paths throughout the landscape. The fate of individuals is determined by their location in the landscape as well as their access to resources (the quantity and quality of habitat in their territory). Habitat quality pixel values from the habitat map (5 m^2) were generalized into a hexagonal grid (780 m^2) by HexSim.

The population cycle implemented in HexSim simulated females only and used discrete-time events. Following a winter survival event, all individuals were transitioned to adult status and adjusted the bounds of their territories to include more or greater quality habitat if available. In the summer, three successive breeding, movement and survival events occurred. During each of the three summer intervals, kangaroo rats reproduced, the youngest stage class dispersed from their natal territory, mortality was imposed, and boundaries of territories were adjusted (Fig. 2).

Strong annual population fluctuations caused by environmental stochasticity were approximated using variation in overwinter survival rates. Mark-recapture studies estimating overwinter survival rates in active dune habitat in favorable (Teucher, 2007) and harsh winters (Gummer, 1997) were used to estimate a normal distribution of overwinter survival rates (mean of 0.48; standard deviation of 0.13). One hundred rates were selected at random from the distribution and supplied to the population model. At the onset of each winter, an overwinter survival rate was selected at random (with replacement) and assigned to the population.

Short gestation, lactation and maturation periods allow juveniles to produce one or two litters during their first year (Day et al., 1956; Duke, 1944; Gummer, 1997; Jones, 1993; Smith and Jorgensen, 1975). Reproduction was modeled as occurring in three distinct pulses wherein juveniles born in the first two breeding pulses were able to mature and produce offspring in the subsequent breeding period. Adult (1.46; 95% CL 1.44–1.48) and juvenile-specific (1.14; 95% CL 1.09–1.21) reproduction rates were estimated using a mean litter size of three (derived from counts of embryos and placental scars from museum specimens; Gummer, 1997), the proportion of reproductively active females (adult 97%; 95% CL 96–98% and juveniles 76%; 95% CL 71–81%) Gummer unpublished data), and assuming an equal sex ratio. Only individuals that held territories were able to reproduce.

Kangaroo rats are solitary, territorial and defend burrows and food caches (Bartholomew and Caswell, 1951; Daly et al., 1984; Eisenberg, 1963; Garner, 1974). After birth, the youngest class of juveniles disperse in search of their own territories. The distribution of dispersal distances for Alberta's kangaroo rats is highly skewed (median of 100 m; Gummer, 1997) with a maximum of ~8.5 km recorded for a single movement. Roads may facilitate kangaroo rat movement (COSEWIC, 2006). Therefore, an intermediate level of autocorrelation in path direction was used to provide forward momentum and simulated individuals were given a slight preference to travel along roads or within habitat rather than through the matrix. Dispersal path lengths were assigned at random to individuals, drawn from a uniform distribution with a maximum of 8.5 km. Individuals stopped before they reached their assigned path length if they came across one hexagon of marginal quality (e.g. road-side habitat) or better. Early stopping truncated movement distances and produced an overall simulated path length distribution that approximated that of the field data. Mechanistic density dependence emerges as individuals spend more time searching for a territory during times of high population density. Movement itself does not incur mortality; however, individuals that require longer dispersal distances to find an unoccupied territory are less likely to acquire sufficient resources for survival.

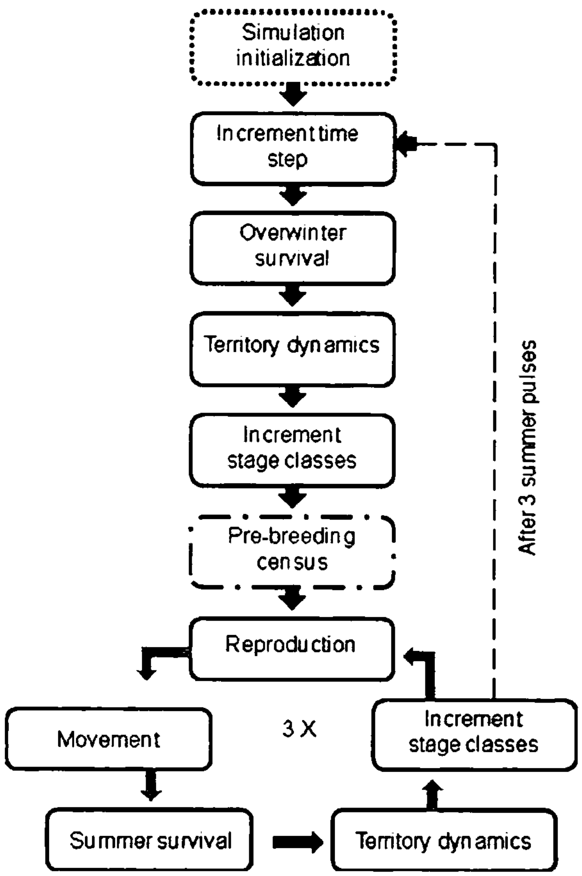

Fig. 2. Kangaroo rat population cycle as implemented in HexSim.

When individuals reached their maximum dispersal distance or came across suitable habitat, the immediate area (23,400 m^2 representing double the maximum possible territory size) was explored for prospective territories. The territory with the greatest resources was then occupied until death. Individuals had to establish a territory that exceeded a minimum resource requirement (10% of the target resource level). If a suitable territory was not available, the individual continued searching during the next movement event. Territories had to meet or exceed the target resource requirement for the occupant to receive the maximum possible overwinter survival rates. As high quality habitats contain the greatest density of resources, little area is required to meet the resource target and territory sizes can be comparatively small. The average home range of radio-collared kangaroo rats is 1750 ± 620 m^2 (±1 SE; Gummer and Robertson, 2003a) in active dune habitats; this home range size was doubled to account for the space occupied by an equal number of males in the population. Thus, ideal territory sizes were at least 3500 m^2 (4.49 hexagons) in high quality habitat (100%). Individuals that occupied territories that met the threshold resource target (4.49 hexagons * 100 quality score = 449), using up to a maximum of 15 hexagons, received the maximum possible overwinter survival rates. As habitat quality decreases, territories must expand to include a greater amount of habitat with lower resource density to reach the same target. Those unable to meet the resource threshold received penalized survival rates that declined linearly to zero as acquired resources declined from an optimal value.

Summer survival rates were provided by Teucher (pers. comm.), based on unreported data from his 2007 study (0.80 for adults, 0.64 for juveniles), and were applied to all individuals occupying territories in each of the summer survival intervals.

2.4. Simulations

Habitat patches were predicted to differ both in their local productivity and contribution to regional population persistence. If so, these differences would provide the basis for the prioritization of habitats for conservation. In our simulations, the productivity of local populations (births–deaths) resulted from the interaction of individual behavior with patch characteristics including size, distribution of quality, isolation, shape and orientation. As such, productivity provides a measure of the contribution of specific patches to regional population abundance. Long-term habitat productivity was calculated by subtracting the total number of deaths from births (and dividing by 100 simulation repetitions). Habitat patches with productivity scores greater than 0 (i.e. sources) were considered to be of greater conservation value than unproductive patches (i.e. sinks).

The relative contribution of habitat components to regional population persistence was assessed by simulating the risk of population extinction under alternative habitat removal scenarios. Due to the large number of patches in the case study landscape, iterative removal of individual patches was not feasible. Instead, groups of habitat patches were iteratively removed based on their habitat quality classification or their productivity (sources versus sinks). The latter quantified the impacts of local productivity on regional population viability. The relative contribution of habitat components to extinction risk was assessed by comparing the amount of habitat that was required to be removed for a 1% change in the probability of extinction (PE), or the proportion of simulations in which there were no females at some point in time.

While many uses of population viability modeling are focused on predicting the future trajectory of a species, our approach is aimed at evaluating the relative potential of existing habitats to support persistence. Therefore, simulations were initialized with the landscape saturated with 25,000 randomly seeded females. Before data were recorded, the population was allowed to stabilize (50 years) and approach a realistic population size of 250 females in the early spring, pre-breeding census. As the demographic value of a habitat may only become clear in the long-term after being subject to environmental stresses (Garshelis, 2000; Pelton and Manen, 1996), 100 years of data were simulated to estimate productivity and risk of extinction. Extinction risk simulations were replicated 1000 times, however the replication of habitat productivity data was limited to 100 iterations due to computational constraints.

We also sought to investigate whether sufficient habitat (of any quality) was available for the long-term persistence of the regional population. A range of population parameters (including dispersal distances, summer survival and reproduction rates) were evaluated in a sensitivity analysis to assess the reliability of conclusions generated from model outcomes. The sensitivity analysis also explored a range of habitat quality values for secondary habitat types as a means of exploring the influence of parameter uncertainty on model outcomes. The population model did not include genetics, sex structure, or allee effects; therefore, predictions at low population sizes may be unreliable (Akcakaya, 2000; IUCN, 2008). To account for this, extinction risk was also expressed as the probability of the regional population falling below the population size thresholds of 50 and 25 female kangaroo rats at least once during the 100 year simulation (Akcakaya, 2000; Ginzburg et al., 1982). As little is known about kangaroo rat population dynamics at very small population sizes, several arbitrary extinction thresholds were examined *a posteriori*. The results of thresholds above 50 females differed little from those at this threshold and were therefore excluded from the analysis. Scenarios that resulted in a probability of extinction (PE) of >10% in 100 years (criteria for a risk status of near threatened; IUCN, 2008) and >20% probability of the population falling below 50 or 25 females were deemed as unlikely to ensure long-term population persistence.

3. Results

3.1. Productivity

Source habitats were generally found within the sand hills regions and consisted primarily of natural habitats (80%). Virtually all of the active dunes performed as highly productive sources and the largest dune in the study area was also the most productive patch in the landscape (Fig. 3). Sink habitats were located throughout the range and consisted primarily of exposed soils (82% by area), as well as semi-stabilized dunes and road-side habitats. Exposed sandy soils accounted for all of the most severe sinks (productivity $\leqslant -100$). As kangaroo rat habitat comprised only a small fraction of the study area (<2%), the majority of the landscape remained unoccupied.

3.2. Habitat removals

In order to predict the relative contribution of habitat types to population persistence, all habitat patches of active dune, semi-stabilized dune, road-side habitats, as well as source and sink habitats were iteratively removed. Probability of extinction in the model was most sensitive to the removal of natural habitat (i.e. actively eroding sand dunes) with the PE increasing by 1% for every 1.7 ha removed (Table 2). The removal of comparatively larger areas (7.4 ha for semi-stabilized dunes and 15.3 ha for road-side habitats) were required to achieve a similar 1% increase in the probability of extinction. Extinction risk was relatively insensitive to the removal of exposed slopes, requiring approximately 37 times the amount (63.7 ha) as actively eroding dunes to produce a 1% increase in the probability of extinction. A large proportion of habitat (39%) was comprised of sinks, and their removal reduced the risk of extinction from a baseline PE of 23.4% to 20.7%.

3.3. Extinction risk and sensitivity analysis

In the baseline landscape (i.e. no patch removals), extinction risk was high with a PE > 10% and with the regional population size falling below 50 and 25 females in 100% and 95% of the simulations respectively (Fig. 4). The overall extinction risk outcomes were

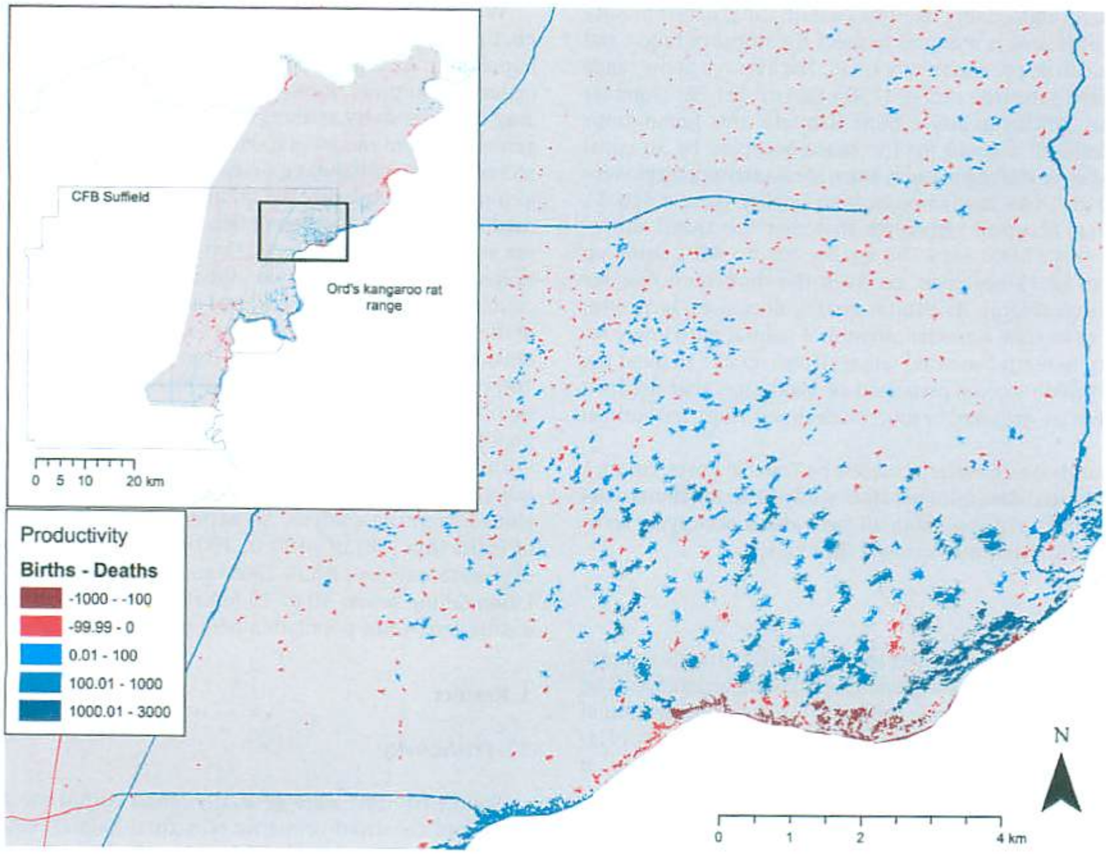

Fig. 3. Predicted long-term productivity of local Ord's kangaroo rat populations in a subset of their range in Alberta, Canada. Source habitats appear in blue, while sink habitats appear in red.

Table 2
Habitat type and productivity removal scenarios: Predicted probability of extinction (PE) and relative contribution to extinction risk.

Removal scenario	Area removed (ha)	PE	Hectares removed for 1% Δ in PE	Rank
Habitat type				
Active dunes	68.3	40.3	1.7	1
Semi-stabilized dunes	550.0	74.2	7.4	2
Exposed soils	1750.4	27.5	63.7	6
Roads/road-sides	424.1	27.8	15.3	3
Productivity				
Sinks	1097.9	20.7	51.8	5
Sources	1694.9	72.0	23.5	4

largely insensitive to a range of population and habitat quality parameter variations. Extinction risk was most sensitive to decreases in survival and reproductive rates, as measured by the absolute value change in PE/percent change in the parameter value (Table 3). Increases in vital rates were not as influential; however, some scenarios resulted in probabilities of extinction less than 10% although the probabilities of falling below 25 and 50 females remained high (67.4–98.4%). Extinction risk was relatively insensitive to changes in maximum dispersal distance.

The model outcomes were relatively insensitive to changes in secondary and semi-stabilized sand dune quality with all scenarios resulting in extinction risk probabilities for thresholds of 50 and 25 females ranging between 88% and 100%, and probabilities of extinction exceeding 10%.

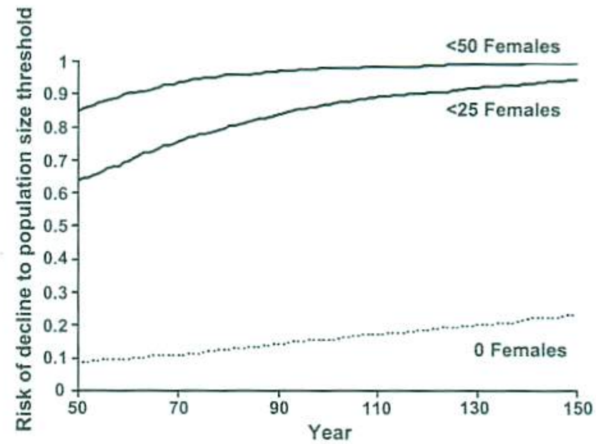

Fig. 4. Cumulative risk of population decline to size thresholds of 0, <25, and <50 female Ord's kangaroo rats for the baseline (pre-removal) landscape.

4. Discussion

Our approach for integrating a habitat map (i.e. RSF-based occurrence model) with population dynamics proved effective for identifying the relative contribution of each habitat type to population viability, thereby providing a straightforward method for ranking and prioritizing habitats. Predictably, the results of habitat removal and productivity simulations suggest that the

Table 3
Local sensitivity analysis of population and habitat quality parameters and resulting risk of the population dropping to size thresholds of <50, <25 and 0 females. Sensitivity was calculated as the absolute Δ PE/percent Δ in parameter value.

Scenario	Risk of decline to population size threshold (%)				
	<50 Females	<25 Females	0 Females (PE)	Sensitivity	Rank
Baseline scenario	99.8	94.9	23.4	–	–
Summer survival					
−10%	100	99.9	92.0	6.86	2
−5%	100	99.8	58.2	6.96	1
+5%	98.3	83.9	8.6	2.96	4
+10%	93.4	67.4	2.9	2.05	6
Reproduction rates					
−10%	100	99.3	56.0	3.26	3
−5%	100	98.5	37.8	2.88	5
+5%	99.7	92.1	15.0	1.68	7
+10%	98.4	85.8	8.7	1.47	9
Max. dispersal distance					
7 km	99.8	96.3	25.8	0.13	15
10 km	99.7	95.1	23.1	0.02	16
Quality of secondary habitat					
−10%	100	99.7	35.3	1.19	10
−20%	100	100	55.3	1.6	8
Semi-stabilized dune quality					
40%	100	99.5	42.4	0.95	11
50%	99.8	98.1	31.9	0.85	12
70%	99.6	93.2	20.2	0.32	14
80%	88.5	88.9	16.3	0.36	13

highest quality habitats in our case study, natural sand dunes, provide the greatest contribution towards long-term persistence and recovery of the Ord's kangaroo rat. In our model, the removal of active dunes produced the greatest effect on regional extinction risk. While these patches represented only a small fraction of the landscape, they contained the most productive habitat patches in the landscape and appeared to drive the dynamics of this population. Semi-stabilized sand dunes are in close proximity to primary active dune habitat and may provide refuge for emigrants. This habitat type ranked second in its relative contribution to population persistence and included many highly productive areas. While the contribution of natural habitat types to persistence was predictable at this coarse scale, the productivity of local habitat patches was less so. Semi-stabilized dune productivity was likely influenced by patch size, spatial effects, and population dynamics.

Approaches to assessing important habitats often assume that all suitable habitat patches contribute to population persistence, particularly if habitat models are based solely on an occurrence model. In contrast, our model results indicate that not all patches and habitat types made substantive contributions to the persistence of our study species. Despite being a pervasive element in the landscape, the removal of exposed soil habitats had a minimal influence on extinction risk, and hence these habitats do not appear to be essential for long-term kangaroo rat persistence. Our approach also demonstrated that some habitats may actually be detrimental to persistence. While sink habitats may temporarily bolster the regional population size (Dias, 1996; Pulliam, 1988), the removal of all sink habitats from the kangaroo rat landscape improved overall population persistence. The correct identification of sink habitats is essential when identifying and protecting habitat, especially if field studies happen over a short period of time when the regional population size happens to be high and sink habitats are occupied. Approaches that fail to link demographic data or dynamics with habitat models may actually undermine conservation efforts by erroneously identifying sinks as important habitats for protection.

The contribution of anthropogenic habitats to kangaroo rat viability has been contentious. In Alberta, kangaroo rats are commonly found along road-sides, particularly during the late-summer population peak. However, road-side habitats are expected to be low quality habitats that represent population sinks as they are associated with greater soil compaction, colder burrow temperatures, greater predation risk, inadequate forage, and lower rates of survival than natural habitats (COSEWIC, 2006; Teucher, 2007). Overall, road margins made a minor contribution to population persistence and patches acted as both population sources and sinks. However, it is unclear why some roads are productive and others are not. In addition, the productivity of road-side habitats can be inconsistent. In our model, the relative quality among habitat types was parameterized using survival data from a year that was observed to have higher than average survival. Thus, it is possible that the data is not representative of a typical year and may overestimate survival and the quality of secondary habitats, particularly in anthropogenic habitats. In the sensitivity analysis, reductions in secondary habitat quality by 20% resulted in many secondary habitat sources, including productive road-sides near high quality dunes, becoming sink habitats. This suggests that the productivity of road-side habitats is particularly variable and unpredictable. Further, these anthropogenic features may alter dispersal patterns because of their linear and pervasive nature in the landscape. While some roads might actually be placed to connect naturally isolated active sand dunes and increase kangaroo rat dispersal, it is unclear whether this benefit would outweigh the potential concerns associated with roads which include increased exposure to predators and parasites. Negative effects of roads might be especially acute if roads are placed between patches of natural habitat, thereby intercepting animals that might have otherwise dispersed between natural habitat patches, placing them in much lower productivity habitat. More research may be required to elucidate these complex influences.

The use of a population viability framework provided a means to investigate whether sufficient habitat was available for the long-term persistence of the species. Other habitat-modeling approaches, such as those based on occurrence models, are typically not capable of providing this assessment. However this question is at the heart of critical habitat identification, where the aim is to determine which habitats are required for the long-term persistence or recovery of a species. Frequent regional extinctions in our simulations suggest that insufficient habitat exists for the long-term persistence of the Ord's kangaroo rat. This conclusion was robust to a range of population and habitat quality parameter scenarios explored in the sensitivity analysis. Thus, not only is current habitat in Alberta likely to be insufficient to support the population, the restoration of existing habitat is likely to be required. Another key advantage of our approach is that it can be used to identify the most valuable areas to undertake habitat restoration. Patches can be identified based on their size, location, occupancy, or productivity. The effect of restoration to larger or higher quality habitats can be compared by assessing population viability in the alternative restored landscapes. In our case study, semi-stabilized dunes made the second greatest contribution to population persistence. Thus, re-activation of stabilized dunes to actively-eroding habitats may be an effective means of improving population viability, although additional habitat alteration scenarios are needed to determine the most valuable restoration sites. Habitat removal experiments can also provide general insight into the potential efficacy of removing versus adding habitat. For example, a similar increase in kangaroo rat persistence may be attained by adding source habitat as by removing twice as much sink habitat. While the focus of this habitat assessment approach was to identify the productive breeding habitats that contribute to long-term population persistence, the realized contribution of a particular habitat patch through time will depend on future changes to both the habitat and non-habitat components of the landscape. Destruction or degradation of habitat patches, changes to the structure or composition of the intervening matrix, or the introduction of disturbances can reduce the performance of habitats. For example, the disruption of dispersal corridors among highly productive habitats, introduction of movement barriers, or increased hostility of the matrix may affect dispersal success, patch occupancy rates, productivity and ultimately population viability. Therefore, the assessment of critical habitats for species at risk should also consider the identification and protection of non-habitat components of the landscape (e.g. dispersal corridors, disturbance-free buffer zones, etc.) upon which the success of essential habitats rely.

5. Conclusions

In summary, our approach to assessing critical habitat provided several advantages for identifying and prioritizing habitats for conservation. The use of spatially-explicit population viability modeling, combined with habitat removal experiments provided a direct link between habitat components and their predicted influence on regional population persistence. Local productivity also provided a fine-scale estimate of the contribution of habitat patches to persistence and another means of prioritizing habitats for conservation. Using this approach, we were able to investigate whether sufficient habitat existed for long-term persistence, and identify sinks that may be detrimental to population persistence. Approaches to assessing critical habitats that rely on short-term occupancy patterns and do not consider long-term population dynamics may undermine conservation efforts by under- or over-estimating the value of habitat patches. Further, approaches that do not distinguish between occurrence and productivity may erroneously include sink habitats (particularly if habitat is limited or degraded) or fail to prioritize key source habitats, which may undermine the conservation efforts. Where possible, assessments of critical habitat components should be based upon habitat-specific demographic information and population dynamics, particularly in regions of variable habitat quality or for species that may exhibit source-sink dynamics.

Role of the funding source

This research was supported by the Department of National Defence, Alberta Sustainable Resource Development, and the University of Calgary. Parks Canada Agency provided in-kind support. The information in this document has been funded in part by the US Environmental Protection Agency. It has been subjected to the Agency's peer and administrative review, and has been approved for publication as an EPA document. Mention of trade names or commercial products does not constitute endorsement or recommendation for use. Funding was provided by sponsors without any requirement for them to contribute to the study design or the collection, analysis, or interpretation of data.

Acknowledgments

We thank R. Dzenkiw for his valuable GIS assistance and feedback on the construction of the Ord's kangaroo rat model.

References

Akcakaya, R.H., 2000. Population viability analyses with demographically and spatially structured models. Ecological Bulletins 48, 23-38.

Alberta Ord's Kangaroo Rat Recovery Team, 2005. Recovery Plan for Ord's Kangaroo Rat in Alberta. Alberta Sustainable Resource Development, Fish and Wildlife Division, Alberta, Edmonton, Alberta, pp. 28.

Aldridge, C.L., Boyce, M.S., 2007. Linking occurrence and fitness to persistence: habitat-based approach for endangered greater sage-grouse. Ecological Applications 17, 508-526.

Armstrong, D.M., 1979. Ecological distribution of rodents in Canyonlands National Park, Utah. Great Basin Naturalist 39, 199-205.

Armstrong, D.P., 2005. Integrating the metapopulation and habitat paradigms for understanding broad-scale declines of species. Conservation Biology 19, 1402-1410.

Bartholomew, G.A., Caswell, H.H., 1951. Locomotion in kangaroo rats and its adaptive significance. Journal of Mammalogy 32, 155-169.

Battin, J., 2004. When good animals love bad habitats: ecological traps and the conservation of animal populations. Conservation Biology 18, 1482-1491.

Bender, D.J., Gummer, D.L., Dzenkiw, R., 2007. Monitoring Protocol for the Ord's Kangaroo Rat. Alberta Sustainable Resource Development, Fish and Wildlife Division, Edmonton, Alberta.

Bender, D.J., Gummer, D.L., Dzenkiw, R., Heinrichs, J.A., 2010. An Occurrence-based Habitat Model for the Ord's Kangaroo Rat (*Dipodomys ordii*) in Alberta. Alberta Sustainable Resource Development, Fish and Wildlife Division, Edmonton, Alberta.

Bowman, J., Cappuccino, N., Fahrig, L., 2002. Patch size and population density: the effect of immigration behavior. Conservation Ecology 6, 9.

Boyce, M., McDonald, L., 1999. Relating populations to habitats using resource selection functions. Trends in Ecology and Evolution 14, 268-272.

Boyce, M., Mao, J., Merrill, E., Fortin, D., Turner, M., Fryxell, J., Turchin, P., 2003. Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. Ecoscience 10, 421-431.

Carroll, C., Noss, R.F., Paquet, P.C., 2001. Carnivores as focal species for conservation planning in the Rocky Mountain region. Ecological Applications 11, 961-980.

COSEWIC, 2006. COSEWIC Assessment and Update Status Report on the Ord's Kangaroo Rat *Dipodomys ordii* in Canada Committee on the Status of Endangered Wildlife in Canada, Ottawa, vii + 34 pp.

Daly, M., Wilson, M.I., Behrends, P., 1984. Breeding of captive kangaroo rats, *Dipodomys merriami* and *D. microps*. Journal of Mammalogy 65, 338-341.

Day, B.N., Egoscue, H.J., Woodbury, A.M., 1956. Ord kangaroo rat in captivity. Science 124, 485-486.

Dias, P.C., 1996. Sources and sinks in population biology. Trends in Ecology and Evolution 11, 326-330.

Duke, K.L., 1944. The breeding season of two species of *Dipodomys*. Journal of Mammalogy 25, 155-160.

Eisenberg, J.F., 1963. The behavior of heteromyid rodents. University of California Publications in Zoology 69, 1-100.

Falcucci, A., Ciucci, P., Maiorano, L., Gentile, L., Boitani, L., 2009. Assessing habitat quality for conservation using an integrated occurrence-mortality model. Journal of Applied Ecology 46, 600-609.

Fleishman, E., Ray, C., Sjogren-Gulve, P., Boggs, C.L., Murphy, D.D., 2002. Assessing the roles of patch quality, area, and isolation in predicting metapopulation dynamics. Conservation Biology 16, 706-716.

Franken, R.J., Hik, D.S., 2004. Influence of habitat quality, patch size and connectivity on colonization and extinction dynamics of collared pikas *Ochotona collaris*. Journal of Animal Ecology 73, 889-896.

Garner, H.W., 1974. Population dynamics, reproduction, and activities of the kangaroo rat, *Dipodomys ordii*, in western Texas. Graduate Studies, Texas Tech University 7, 1-28.

Garshelis, D.L., 2000. Delusions in habitat evaluation: measuring use, selection, and importance. In: Biotani, L., Fuller, T.K. (Eds.), Research Techniques in Animal Ecology: Controversies and Consequences. Columbia University Press, pp. 111-164.

Ginzburg, L.R., Slobodkin, L.B., Johnson, K., Bindman, A.G., 1982. Quasiextinction probabilities as a measure of impact on population growth. Risk Analysis 2, 171-181.

Gummer, D.L., 1997. Effects of Latitude and Long-term Isolation on the Ecology of Northern Ord's Kangaroo Rats (*Dipodomys ordii*). University of Calgary.

Gummer, D.L., 1999. Distribution and Abundance of Ord's Kangaroo Rats in Canadian Forces Base Suffield National Wildlife Area. Report for Canadian Wildlife Service, Edmonton, Alberta, pp. 29.

Gummer, D.L., Robertson, S., 2003a. Evaluation of Activities and Survival of Ord's Kangaroo Rats during and Post-construction of the North Suffield Pipeline. Provincial Museum of Alberta, Edmonton, AB.

Gummer, D.L., Robertson, S.E., 2003b. Evaluation of Survival and Activities of Ord's Kangaroo Rats: One Year after Construction of the North Suffield Gas Pipeline. Report for Alberta Conservation Association, Edmonton, pp. 14.

Hallett, J.G., 1982. Habitat selection and the community matrix of a desert small-mammal fauna. Ecology 63, 1400-1410.

IUCN, 2008. Guidelines for Using The IUCN Red List Categories and Criteria. Version 7.0.

Johnson, C., Seip, D., Boyce, M., 2004. A quantitative approach to conservation planning: using resource selection functions to map the distribution of mountain caribou at multiple spatial scales. Ecology 41, 238-251.

Jones, W.T., 1993. The social systems of heteromyid rodents. In: Genoways, H.H., Brown, J.H. (Eds.), Biology of the Heteromyidae. American Society of Mammologyists, Provo, pp. 575-595.

Kaufman, D.W., Kaufman, G.A., 1982. Effect of moonlight on activity and microhabitat use by Ord's kangaroo rat (*Dipodomys ordii*). Journal of Mammalogy 63, 309-312.

Kenny, R.J.L., 1989. Population, Distribution, Habitat Use, and Natural History of Ord's Kangaroo Rat (*Dipodomys ordii*) in the Sand Hill Areas of South-western Saskatchewan and South-eastern Alberta. University of Manitoba.
Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L., Erickson, W.P., 2002. Resource Selection by Animals: Statistical Analysis and Design for Field Studies. Kluwer Press, Boston, Massachusetts.
Nero, R.W., Fyfe, R.W., 1956. Kangaroo rat colonies found. Blue Jay 14, 107–110.
Nielsen, S.E., Stenhouse, G.B., Boyce, M.S., 2006. A habitat-based framework for grizzly bear conservation in Alberta. Biological Conservation 130, 217–229.
Pelton, M.R., Manen, F.T.v., 1996. Benefits and pitfalls of long-term research: a case study of black bears in Great Smoky Mountains National Park. Wildlife Society Bulletin 24, 443–450.
Pulliam, R.H., 1988. Sources, sinks, and population regulation. The American Naturalist 132, 652–661.
Schumaker, N.H., 1998. A Users Guide to the PATCH Model. EPA/600/R-98/135. Environmental Protection Agency, Environmental Research Laboratory, Corvallis, Oregon.
Schumaker, N.H., 2008. HexSim (Version 1.3.6.9). US Environmental Protection Agency, Environmental Research Laboratory, Corvallis, Oregon. <http://www.epa.gov/hexsim>.
Smith, H.D., Hampson, M.J., 1969. A kangaroo rat colony in Alberta. Blue Jay 27, 224–225.
Smith, H.D., Jorgensen, C.D., 1975. Reproductive biology of North American desert rodents. In: Prakash, I., Ghosh, P.K., Junk, W. (Eds.), Rodents in Desert Environments. B.V. Publishers, Hague, Netherlands, pp. 305–330.
Stangl Jr., F.B., Schafer, T.S., Goetze, J.R., Pinchak, W., 1992. Opportunistic use of modified and disturbed habitat by the Texas kangaroo rat (*Dipodomys elator*). Texas Journal of Science 44, 25–35.
Teucher, A.C., 2007. Factors Affecting Ord's Kangaroo Rats (*Dipodomys ordii*) in Natural and Anthropogenic Habitats. University of Calgary.
Van Horne, B., 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47, 893–901.